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Approaches and methods for the scientific evaluation of bird and mammal predation on salmon in the Northwest Atlantic

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ABSTRACT

Decreases in numbers of Atlantic salmon returning to North American rivers have prompted interest in methodologies to determine if seabird and marine mammal predation has contributed to this decline. Predation rates on salmon by seals and seabirds (other than gannets) in the Northwest Atlantic are too low to be reliably measured. However, predators could remove a substantial proportion of salmon biomass even if salmon are very rare in their diets, because the biomass of salmon in the sea is very small. Several approaches are proposed to clarify the relation between salmon and their predators. 1) Marine-phase salmon have very high growth and high mortality rates in comparison with other pelagic fishes that occupy the same habitat. The basis of this highly risk-prone life history needs to be examined, including behavioural thermoregulation for growth promotion, temperature effects on ability to avoid predation, and use of schooling as an anti-predator strategy. 2) Examination of predator scars on returning salmon, use of chemical tracers to detect salmon predation, and improved reporting of salmon remains in conventional diet analysis may shed light on salmon interactions with their predators. 3) Exploitation rates of salmon by gannets on the high seas and by birds and seals in estuaries should be measured. 4) The effect of predation on salmon populations, and the consequences to salmon of changes in predator numbers, should be examined through food-web and trophic models. A broadly-based approach encompassing these diverse methodologies is recommended because predator-salmon relations in the sea are complex and are difficult to study directly.

RÉSUMÉ

La diminution des saumons Atlantiques qui retournent aux rivières nord-américaines a stimulé l'intérêt dans les méthodologies qui pourraient déterminer si la prédation par les oiseaux et les mammifères marins a contribué à ce déclin. Les taux de prédation sur le saumon de la part des mammifères et des oiseaux marins (à part celle du fou de Bassan) dans le nord-ouest de l'Atlantique sont trop petits pour être mesurés de façon fiable. Pourtant, les prédateurs pourraient récolter une partie importante de la biomasse des saumons même si le saumon est rare dans leur diète, en raison de la très petite biomasse des saumons dans l'océan. On propose plusieurs approches pour clarifier la relation entre le saumon et ses prédateurs. 1) Les saumons en phase marine ont des taux de croissance et de mortalité qui sont très élevés en comparaison avec d'autres poissons pélagiques qui occupent le même habitat. Le fondement de cette histoire vitale, fortement susceptible aux risques, doit être examiné, y compris la thermorégulation comportementale pour accélérer la croissance, les effets de température sur la capacité d'échapper à la prédation, et l'utilisation des groupes comme stratégie anti-prédateur. 2) L'examen des cicatrices causées par les prédateurs sur les saumons en retour, l'utilisation des traceurs chimiques pour détecter la prédation du saumon, et un meilleur reportage des restes des saumons dans les analyses de diète conventionnelle pourraient jeter de la lumière sur les interactions entre les saumons et leurs prédateurs. 3) Les taux d'exploitation des saumons par les fous de Bassan en haute mer et par les oiseaux et les phoques dans les estuaires devraient être mesurés. L'effet de la prédation sur les populations des saumons, et les conséquences aux saumons des changements dans le nombre de prédateurs, devraient être examinés à l'aide des modèles trophiques et de maille alimentaire. Une approche d'envergure qui couvre ces méthodologies variées est recommandée parce que les relations entre saumon et prédateur dans l'océan sont complexes et difficiles à étudier directement.

Introduction

The prolonged decline in pre-fishery abundance of salmon in the West Atlantic (Anon. 1999a) has spurred interest in research methodologies that could identify the cause or causes of this decline (Dempson and Reddin 2000, O'Neill et al. 2000). Declining salmon returns have coincided with rising populations of seals and some seabird species in eastern Canada (Cairns and Reddin 2000, Hammill and Stenson 2000). This has bolstered suggestions that predation is depressing salmon populations (Anthony 1994, Amiro 1998). The present paper proposes and discusses questions, approaches and methodologies that may lead to improved understanding of the relation between Atlantic salmon and their avian and mammalian predators in the Northwest Atlantic.

In this paper, marine and marine-phase are taken to include estuarine waters.

A brief review of bird and mammal predation on marine-phase salmon

Background

When Atlantic salmon smolts leave fresh water, they enter a new environment with new predators. Potential salmon predators in estuaries and the open sea include both ectotherms (fish) and endotherms (birds, pinnipeds, cetaceans).

Interactions between salmonids and endothermic predators have been most thoroughly investigated on the west coast of the United States, where interest has been prompted by the decline of many salmonid populations to precariously low levels (Anon. 1997). The most detailed study of bird predation in the region has taken place in the mouth of the Columbia River, where Caspian terns and double-crested cormorants appear to take substantial proportions of smolt runs (Roby 1997). This has resulted in attempts to move the colonies to locations where outgoing smolts would be less vulnerable to avian predation.

The main pinnipeds that interact with salmonids on the US west coast are harbour seals and sea lions, whose populations have risen sharply in recent years (Anon. 1997). Harbour seals and sea lions prey on salmonids in estuaries and in rivers. In many rivers, from 10% to 50% of adult salmon arriving at counting facilities bear scars which are attributed to pinnipeds (Harmon et al. 1994, Anon. 1997, Fryer 1998). Pinnipeds penetrate several hundred km inland in some rivers, where they prey on fish including salmonids at the foot of dams (Nash et al. 2000).

Bigg et al. (1990) estimated that pinnipeds harvested 46% of the adult chinook salmon that attempted to enter a Vancouver Island stream; exploitation rate was $\leq$8% for other salmon species. With one exception, in which California sea lions have been shown to reduce a steelhead run, U.S. studies have not determined whether pinniped predation in rivers and estuaries are affecting salmonid populations (Anon. 1997).

Bigg et al. (1990) described hunting behaviour of harbour seals during a salmon run on the basis of visual observations. Seals patrolled small areas of an estuary, apparently searching for salmon. When a salmon was encountered a brief chase occurred, with rapid swimming bursts and frequent sudden turns. Chases were nearly always less than a minute long. Seals typically grasped the salmon on the underside by the throat or belly. Teeth and claws were used to tear out the belly and to break the salmon apart. Most harbour seal attacks on salmon involved two or more seals. The largest salmon taken by seals in the course of this study was a 12.7 kg chinook. Five seals were involved in the attack.

Salmon have been identified in stomach contents of five of the 11 pinniped species inhabiting the eastern Pacific (Fiscus 1980). Although salmon commonly appear in the diets of northern fur seals, an offshore species, predation on salmon seems less intense in the open sea than in estuaries and rivers (Fiscus 1980, Anon. 1997).

Salmon have been reported from stomachs of nine of the 23 cetacean species that occupy salmon waters of the north Pacific, including the harbour porpoise (Fiscus 1980).

Most European studies of avian predation on marine-phase salmon have taken place in estuaries, where birds prey on outgoing smolts (Valle 1985, Reitan et al. 1987, Kennedy and Greer 1988). Atlantic salmon has also been found in gannet diet in Scotland (Wanless 1984).

In Britain, there are numerous reports of harbour and grey seals consuming salmon (Rae and Shearer 1965, Rae 1973, Harwood 1984, Pierce et al. 1991). However, most of these reports come from the vicinity of fishing gear, and probably involve stealing of netted fish. Seal predation on free-swimming salmon is less common, and is thought to occur most often when salmon enter estuaries or swim in concentrations along the coast (Pierce et al. 1997).

Salmon has been reported in the diets of belugas and bottlenose dolphins in the northeast Atlantic (Anon. 1999b). Tomilin (1957, quoted by Fiscus 1980) reported that harbour porpoises also prey on salmon in the Atlantic (location not given).

Northwest Atlantic

The main potential bird predators of Atlantic salmon in estuaries bordering the northwest Atlantic are cormorants and gulls. Smolts comprised 3.3% of recorded diets of double-crested cormorants in the Maritime Provinces during the smolt run (Cairns 1998). However, no samples were available from estuaries of the region's major salmon rivers, so overall predation intensity of cormorants on salmon smolts is unknown.

No studies have apparently been completed of gull diet during times and at locations of smolt runs in northeastern North America, but gulls are common in most estuaries and may feed on smolts.

Cairns and Reddin (2000) compared growth curves of North American post-smolt salmon to maximum prey sizes of seabirds to determine what seabird species would be capable of preying on post-smolts, and when that predation could occur. This analysis indicated that kittiwakes, gulls, murres, shearwaters, and fulmars are potential predators of post-smolts in their first year at sea. Predation could occur from smolt exit to the time when the post-smolts become too large for the birds to consume. This occurs from mid-June to autumn of the post-smolt year, depending on the seabird species. The northern gannet is the region's largest seabird, and can prey on post-smolts until the birds leave the area about mid-autumn (Montevecchi et al. submitted).

Salmon post-smolts appear to be more vulnerable to gannets than to any other endothermic predator in the region. Post-smolts contributed 0.29% and 2.53% of gannet diet on Funk Island, Newfoundland, in August 1977-1989 and August 1990-2000, respectively (Montevecchi et al. submitted). This amounts to 0.22% and 2.70% of estimated total post-smolt biomass for the two periods, respectively. These estimates are for August only, and for a colony that contains about 13% of the region's breeding gannets. Limited sampling has revealed no evidence of salmon predation by gannets that breed in two Gulf of St. Lawrence gannetries in recent years. Gannet diets at the three remaining North American colonies have never been measured.

The only evidence of salmon predation by other seabird species in eastern North America is a single tag found in a common murre stomach in eastern Newfoundland (Montevecchi et al. 1988, Cairns and Reddin 2000).

Seabirds, including gulls and cormorants, are not large enough to feed on salmon in their 1SW year and subsequently. Hence these birds are not a threat to adults returning through estuaries. Osprey and eagles feed on fish in estuaries, but ospreys are probably too small to take an adult salmon, and eagles are generally scavengers rather than active predators. Blair (1956) reported a "fish hawk" eating a dead grilse on the Miramichi, but there is no indication whether the bird captured the fish live.

Harp, hooded, grey, and harbour seals are the four main pinnipeds in the northwest Atlantic. On the basis of size distributions of seal prey and visual observations of seal predation on large fish, Cairns and Reddin (2000) concluded that salmon are of a size that is vulnerable to predation by these species during their entire marine phase.

Evidence that seals eat wild-caught salmon is very rare in the region. Salmon remains or salmon tags have been found in five seal stomachs (one harbour, two grey, two harp), of the many thousands of stomachs sampled in the Northwest Atlantic (Cairns and Reddin 2000). These authors also reported a handful of visual observations of seals eating salmon.

Annual seabird and seal consumption of marine prey in eastern Canadian waters totals about 2.4 million and 4.0 million t, respectively (Cairns and Reddin 2000, based on Diamond et al. 1993; Hammill and Stenson 2000). Biomass of post-smolt salmon peaks in fall at about 1,600 t (Cairns and Reddin 2000). Total harvest by seabirds and seals in the region is thus about 4,000 times greater than maximum post-smolt biomass. Because total seabird and seal consumption is so much greater than salmon biomass, predation by seabirds and seals could remove a high fraction of salmon biomass even if salmon constitute a minute fraction of predator diet. Cairns and Reddin (2000) calculated that, if seabird and seals in eastern Canadian waters consume 100% of post-smolt biomass, then post-smolts would constitute 0.04% of predator diet. Similarly, if seabirds and seals consume 100% of 1SW salmon, then 1SW salmon would constitute 0.03% of predator diet. This means that it is plausible that seabirds and seals are consuming a substantial fraction of salmon biomass, despite the rarity of salmon remains in these predators' stomachs.

Salmon has never been confirmed in any cetacean in the Northwest Atlantic, although Fontaine et al. (1994) found otoliths of an unidentified salmonid in a harbour porpoise stomach. Salmon vulnerability to cetaceans has not been examined in detail. However, size ranges of post-smolts overlap the prey size distributions of most odontocete cetaceans (Anon. 1999b). Annual consumption by cetaceans in eastern Canadian waters is unknown, but is probably substantial given the large consumption estimates for nearby areas (1.9 million t for U.S. Northeast Shelf, Kenney et al. 1997; 6.3 million t in waters around Iceland, Sigurjonsson and Vikingsson 1998). It thus appears probable that cetaceans, like birds and seals, could harvest a substantial fraction of salmon biomass even if salmon is a very small portion of their diet.

Approaches to salmon-predator interactions

In the marine environment, Atlantic salmon are a rare species in a complex web of trophic interactions. Consequently, gaining understanding of the relations between salmon and their predators is a major challenge. Four potential approaches are outlined below.

Life history and behaviour of marine-phase salmon

Life history strategies

There is a remarkably large literature which examines life history patterns and strategies of Atlantic salmon (e.g. Hutchings and Jones 1998 and references therein). However, in nearly all of these studies only intra-specific comparisons are made. In studies with inter-specific comparisons, the reference species are other salmonids (e.g. Fleming 1998).

Fundamental understanding of the predator-prey relations of marine-phase salmon is unlikely to occur without basic knowledge of the nature of the species' life history while at sea. As pelagic fish, salmon in the northwest Atlantic share their habitat with other pelagic finfish, notably herring, mackerel, and capelin. Salmon are vastly different from these species in growth and mortality rates. Herring and mackerel at age 3-4 typically grow 20-30% in weight annually (Scott and Scott 1988). In contrast, salmon increase in weight 76-fold between smolt exit and return as 1SW fish the following year (Cairns and Reddin 2000). This means that post-smolt salmon grow ~200 times faster than herring and mackerel. Marine fish of the approximate size of post-smolts typically have annual survivorships in the range of 60%, according to weight-based allometric equations (Lorenzen 1996). Salmon return rates between smolt and 1SW return are currently under 5% in most locations in the northwest Atlantic (Cairns and Reddin 2000), but even when salmon survival was much higher, return rates were far lower than 60%.

Salmon are doing something very different than other finfish that occupy the same habitat. Given their extreme growth rates and high mortality, it seems reasonable to characterise them as risk-prone. But what behaviours put them at risk, and how are the rewards dispensed if they win the bet? The apparent rapid vertical oscillations of marine-phase salmon (Sturlaugsson 1995, Reddin et al. 1999) may offer a clue. The major determinants of growth in fishes are temperature and food supply. Salmon may be using the warm surface layer to increase their internal temperature, and therefore their growth rate, while periodically descending to depth to forage. This would be a form of behavioral thermoregulation, analogous to basking in reptiles. But predation risk is probably highest in the surface layer where strong illumination facilitates prey detection by predators. Experiments with growth-enhanced transgenic salmon have suggested that fish with rapid growth are willing to accept higher predation risk to achieve such growth rates (Abrahams and Sutterlin 1999). Thus salmon appear to be trading off the growth benefits of occupying the surface zone against its increased predation risk.

The decrease in numbers of salmon returning to rivers has not been accompanied by a decrease in size. At some sites size of grilse has increased (Chaput et al. 1999). This suggests that salmon are willing to undergo a higher-than-normal risk of mortality in order to maintain growth rates.

There are several approaches that may help clarify the nature of the Atlantic salmon's marine-phase life history. Further use of archival tags, especially if depth as well as temperature can be recorded, will elucidate behaviour patterns of salmon of sea age 1 or greater. This approach requires an animal that is large enough to carry the instrumentation, and the opportunity to capture and recapture it. This is most likely to be the case for kelts, and least likely for post-smolts which can carry only small instrument packages and which are difficult to re-capture. Data from salmon gillnet and trawl surveys may shed further light on patterns of vertical distribution in the water. Data from these sources would be most useful if simultaneous information on salmon diet and on vertical distribution of salmon prey is collected.

Some predictions arising from life history considerations could be directly tested by observations of post-smolt salmon in sea cages (Juell 1995). Predictions and tests follow:

a) It is hypothesised that predation risk is highest in the warm surface layer because this is the layer that is best illuminated. However, warm water may also increase swimming performance, increasing the chances that predator attacks will be evaded. The relative influences of temperature and illumination on predator attack rate and attack success could be evaluated through experiments involving bird or seal predators.

b) In a thermally stratified environment in which food is offered below the thermocline, salmon ought to spend most of their time at the surface, but descend as necessary to feed. Time spent in the warm surface layer ought to be adjusted to provide the growth rate needed to reach target sizes of typical 1SW or 2SW returnees. These predictions could be tested by measuring growth and behaviour in sea-pens or tanks.

c) Marine-phase salmon ought to be willing to feed at a higher level of exposure to predator models (e.g. Gotceitas and Godin 1993) than are herring, mackerel, or juvenile salmon in fresh water.

d) Post-smolts that are underfed ought to be willing to feed under a higher predation risk than are post-smolts that are adequately fed. Underfed salmon should increase their time spent in the warm surface layer in order to increase growth rate. Fish that are given food in over-abundance ought to decrease time spent in the surface layer.

e) Post-smolts appear to be most numerous in the top metre or so of the water column (Dutil and Coutu 1988). There would seem to be no thermal advantage of doing this, because the warm surface layer is typically many metres deep. The possibility that post-smolts are in this surface zone to feed needs to be investigated.

If highest predation risk occurs in the warm surface layer, and if increases in predation in this layer has contributed to the decline in salmon returns, then salmon return rates ought to be related to characteristics of the surface layer. One prediction is that return rates should be positively correlated with the thickness of the surface layer. Thus in years where the surface layer is thin, salmon should be held close to the surface, where predation risk is presumed to be highest, to acquire the thermal advantage they need to maintain target growth rates.

Temperature

Success of predatory attacks depends heavily on reaction time, speed, and manoeuvrability of predator and prey during the short period of time before and during the attack. Seabirds and marine mammals of the northwest Atlantic are endotherms which have heavy insulation and other adaptations to life in cold water. Therefore their swimming performance should show little or no dependence on water temperature. Salmon are ectotherms, so their performance declines with cooler temperatures.

The impact of temperature on success of endothermic predation on ectothermic fish has not been thoroughly examined, although several authors have noted that fish tend to hide under cover or become nocturnal at low temperatures, apparently to reduce risk of predation (Frederick and Loftus 1993, Fraser et al. 1995, Valdimarsson and Metcalfe 1997, Greenwood and Metcalfe 1998).

The past decade has seen significant fluctuations in temperature regimes of marine waters occupied by Atlantic salmon (Colburne 1999). Changing global climates may lead to further changes (IPCC 1995). It is therefore important to know if changes in ambient temperature will shift the balance between salmon and their endothermic predators.

The first step in investigating the thermal ecology of endotherm predation on salmon is to determine the relation of reaction time, swimming speed, and manoeuvrability to ambient temperature. Fish commonly display metabolic compensation to reduce the depressing effects of low temperature on performance (Evans 1990), but such mechanisms only partly offset temperature effects (Johnston et al. 1991). Booth et al. (1997) reported that wild adult salmon showed higher sustained swimming speeds at 18°C than at 12°C, but peak speeds over 10 second intervals did not differ between these temperatures. Predation encounters between salmon and pinnipeds are generally short (Bigg et al. 1990), hence swimming performance over brief periods of time are critical to chances of escape. The constancy with temperature of speeds during 10 second intervals as reported by Booth et al. (1997) is unexpected given the general decline of swimming performance with temperature in fish (Wardle 1980). Hence this experiment should be repeated, and other measures of swimming performance, including reaction time and manoeuvrability, should be tested across a range of temperatures.

The ambient temperature of a salmon depends on its position in a thermally stratified water column. Salmon fitted with archival thermograph tags commonly show spiked temperature profiles, suggestive of short-term movements between the warm surface layer and colder water underneath (Sturlaugsson 1995, Reddin et al. 1999). Such studies should be expanded, with comparison to simultaneously measured temperature profiles to clarify vertical migrations of salmon across thermal layers. If salmon move between water layers of differing temperatures at short intervals, body tissues will take a period of time to warm or cool to the new ambient temperature. Thus effects of thermal "inertia" may be important in determining temperature-mediated swimming performance. Theoretical models should be developed and experiments with real fish should be performed to determine time required for body tissues to reach ambient temperatures.

Schooling

Salmon tend to occupy the surface layer of the ocean (Dutil and Coutu 1988). Because there is no cover in this habitat, pelagic fish reduce predation risk by forming schools (Peuhkuri 1997, Sogard and Olla 1997). In general, protection against predation decreases with declining school size (Krause et al. 1998). Parkinson (1991) reported experimental evidence that juvenile chinook salmon in low densities have difficulty in locating each other to form schools. This means that fish that become rare may suffer increased predation risk because their ability to form schools is impaired. Risk due to insufficiency of school size is potentially greatest in the southern parts of Atlantic salmon range, where output of smolts, or at least of wild-reared smolts, has declined markedly.

Although there is some evidence that post-smolt salmon tend to cluster in the marine environment (Dutil and Coutu 1988, Holm et al. 1992, Holst et al. 2000), schooling behaviour of marine-phase salmon is not well understood. Data sets from pelagic salmon studies should be examined to evaluate the aggregative tendencies of post-smolt salmon. If post-smolts actively attempt to form schools, but school size is constrained by difficulty in finding conspecifics, then school size should be small in early morning and increase throughout the day. Data from surveys directed at other pelagic fishes should also be examined to determine if post-smolt salmon school with other species.

Aggregative tendencies of post-smolts could be evaluated by monitoring movements and behaviour of

post-smolts by means of telemetry, archival tags, underwater video, and hydroacoustics (Joerstad et al. 1994, Holm et al. 1992, Boehlert 1997, Anon. 1998). Such data would also help clarify post-smolt movement patterns, which would assist in determining whether post-smolts of various stocks have the opportunity to school together.

The anti-predation advantages of schooling could be measured experimentally by introducing post-smolts and predators into large cages. Effects of school size could be measured by measuring predation success with varying school size.

Methods to investigate predation ecology

Scarring

Predation by seals on salmon is generally not directly observed. However, salmon which survive attacks by seals and other predators often bear scars, which may offer insight into the nature of this predation.

The first requirement of any study of scars resulting from marine predator attacks is reliable identification of such marks. Harmon et al. (1994) and Fryer (1998) classified pinniped-induced marks as a) claw rake abrasions in the form of scratches on the flanks, b) canine teeth abrasions in the form of arched scratches, and c) bite wounds. However, these authors did not systematically examine alternative explanations to these marks. Likewise, other workers (Rae and Shearer 1965, Harwood and Greenwood 1985, Baum 1997) assume that puncture or rake wounds are seal-induced. Thompson and MacKay (1999) found that marks on salmon returning to a Scottish river commonly consisted of five or more parallel lines with similar inter-scar spacing. They attributed these marks to the regularly spaced homodont teeth of odontocete cetaceans, and argued that many of the marks attributed in the literature to seals may be due to cetaceans instead. Welch et al. (1991) reported that many surface marks on Pacific salmon are probably due to attacks by the daggertooth (*Anotopterus pharao*), a bathypelagic fish.

Preliminary data on surface marks on salmon returning to the Saint John River and to rivers in Quebec and Labrador have been obtained from the 1999 season (D. Cairns, D. Sutherland, S. Ratelle, D. Reddin, S. Tremblay, F. Whoriskey, and L. Marshall, unpubl. data). Some salmon, particularly on the Saint John, had puncture wounds in matching positions on either side of the belly, which appear to be consistent with the canine teeth of a heterodont predator (seals). Many returning salmon bore marks in a variety of positions on the body. Generally these marks did not show matching holes or parallel grooves which could be interpreted as the result of teeth or claws. The origin of these marks is uncertain.

Criteria for identifying predator-induced marks can be inferred from examination of mark patterns and comparisons with gape and claw characteristics of potential predators (c.f. Thompson and MacKay 1999). However, to have full confidence in identification criteria, experiments should be conducted in which captive predators are given access to live adult salmon. Patterns of marks resulting from unsuccessful attacks can then be examined. If water visibility is good, pattern of initial wounds could be recorded even if attacks are eventually successful. Because predatory behaviour may vary among species, this experiment should be conducted with all the seals species that occur in the area of interest, and with other potential predators as available.

Returning adult Atlantic salmon are checked at numerous counting facilities in eastern North America. With the establishment of reliable criteria for identifying predator-induced marks, managers of counting facilities should be encouraged to record such marks according to protocols that are standardized across the region. This will allow direct comparisons of scarring rate among rivers.

Time series of surface marks have been maintained at some counting facilities. Depending on the categories of marks that have been recorded, it may be possible to plot changes of predator-induced scars with time, or to convert historic data into rates of predator-induced scarring that are directly comparable to rates calculated under the new criteria. If rates of predator-induced scarring are correlated with rates of lethal attacks, then these time series may provide an index of changes in predator-induced mortality rates over time.

Comparisons of scarring rates among rivers may identify rivers with high predator activity, which may in turn suggest sites for more detailed studies leading to estimation of exploitation rates.

Marks on returning salmon are a mix of fresh wounds showing raw flesh, and old wounds that are healed over (Cairns et al. unpubl. data). It may be possible to establish the age of healed scars by analysis of scales that have re-grown at the site. Analyses of Sr:Ca ratios in otoliths have been used to infer histories of temperature, salinity, growth, and maturation (Anon. 1999c). Application of such techniques to scales regrown in scars might lead to inferences as to location of the attack.

In Scotland, predator marks are less frequent on grilse than on large salmon (Rae and Shearer 1965). In the west coast of the United States, small "jack" salmon lack pinniped-induced scars, while large salmon returning to the same rivers have high scarring rates (Anon. 1997). These differences are interpreted as meaning that small adult salmon have a lower chance of surviving seal attacks than do large salmon. In eastern Canada, rates of apparent seal-induced

scaring also appear to be higher on large salmon than on small salmon (D. Moore, D. Sutherland, and L. Marshall, pers. comm.).

The differential between scarring rates on small and large salmon offers a means to calculate the minimum mortality rate due to predation (L. Marshall pers. comm.). If migration routes, timing, and behaviour of small and large returnees is the same, and if marine mammals attack the two groups at the same frequency, then the difference in recorded scarring rates may be due to superior escape performance of large salmon. Under these assumptions,

$$S_l - S_s = M_a,$$

where S_l = scarring rate of large salmonid, S_s = scarring rate of small salmon, and M_a = rate of attacks that are lethal to small salmon, but which large salmon would have been able to survive.

Some large salmon presumably die in marine mammal attacks, at a rate of M_l. Total marine mammal-induced mortality to small salmon is

$$M_a + M_l$$

because attacks that are successful against large salmon would presumably also be successful against small salmon.

Because M_l is unknown, the rate that can be calculated from scarring rate differences (M_a) is a minimum estimate of total small salmon mortality.

The ultimate goal of scar investigations would be to estimate total mortality due to marine mammals. To do this we would need to know the success rate of attacks. Success rates could be measured in tanks, but such rates may not closely resemble those that occur in the wild. In circumstances where there is clear water and good vantage points, it may be possible to directly observe attacks on salmon and record their outcome (e.g. Bigg et al. 1990). However attack outcomes in such circumstances may differ from the overall mean, because the conditions that make it easy for the observer to see (i.e. clear water) will also affect the salmon's ability to detect and escape the attack.

Predator diet studies

Diet studies of predators (other than gannets) in the open sea are unlikely to lead to reliable determination of predator exploitation rate on salmon, because the incidence of salmon in diet is too low to be reliably measured. However, when salmon remains are found, they should be documented and reported. Studies of predator diets commonly emphasize abundant prey and pay less attention to rare prey. Two studies of seal and seabird diet in the northwest Atlantic found evidence of salmon predation but did not report it; the information was later transmitted as personal communications (Reddin and Cairns 2000). This suggests that the need to fully report salmon remains in predator diets should be promoted among those responsible for such studies. Reference salmon otoliths should be provided where needed.

Chemical detection of salmon in predator tissue

Prey may have species-specific chemical signatures which can be detected in tissue samples of prey by serological or other techniques (Pierce et al. 1990). However, the rarity of salmon in diet of seabirds and seals means that chemical indicators of salmon will exist at very low concentration. To be broadly useful, any method to detect salmon consumption in a predator's diet will have to be capable of detecting salmon or its metabolites at very low levels.

Exploitation rate

Duffy and Schneider (1994) proposed that seabird predation impact could be evaluated through a series of ratios, including the proportion of standing stock removed by the birds, the proportion of annual production removed by birds, and the ratio of bird harvest to fishery landings. Of these, proportion of standing stock harvested (exploitation rate) seems most appropriate for Atlantic salmon whose standing stocks can be estimated and which is not presently subject to substantial removal fisheries. The standard way to estimate exploitation rate of a predator on a prey is to:

1) measure the proportion of predator diet consisting of the prey,

2) calculate the total quantity of the prey removed by the predator by bioenergetic modelling,

3) estimate the total prey biomass, and

4) calculate the exploitation rate as consumption of prey in question/prey biomass.

Calculation of salmon exploitation rate does not appear to be feasible for seabird and seal predators at broad geographic scales in the northwest Atlantic, because major impacts on salmon would occur even when salmon predation is too rare to reliably measure. (Gannets are an exception; Montevecchi et al. submitted). For example, if seabirds and seals harvest 10% of the post-smolt salmon population of the Northwest Atlantic, only one out of 22,336 prey items would be a salmon (Cairns and Reddin 2000). This means that sample sizes in the hundreds of thousands would be required to accurately measure 1) above. Such sample sizes are beyond the realm of the possible.

We are thus faced with the impracticality of directly estimating exploitation rate of most predators on salmon at a scale of the Northwest Atlantic. However,

exploitation rate could be estimated for gannets, and in some estuaries where salmon contribution to diet may sufficiently high to measure.

Gannets

Gannets breed in three colonies in eastern Newfoundland and three in the Gulf of St. Lawrence; an incipient colony in the Bay of Fundy had a single nest in 1999. Diets of gannets can be readily and non-destructively sampled by approaching birds and inducing them to regurgitate. Such regurgitates are usually fresh and easily identified to species.

The time-series of gannet diet data from Funk Island, Newfoundland, that was initiated in 1977 (Montevecchi et al. submitted) should continue, and be expanded to other colonies. Sampling should begin after smolt exit (beginning of June) and continue to the departure of gannets from the region (mid-fall). Because of access considerations, diet data can be most readily obtained from Bonaventure Island and Great Bird Rock in the Gulf of St. Lawrence and Cape St. Marys and Funk Island in Newfoundland.

Diet data with good temporal and spatial coverage, in conjunction with bioenergetic modelling and estimates of post-smolt biomass, will allow calculation of the exploitation rate of gannets on the total post-smolt cohort in the northwest Atlantic. Data obtained from gannets will also clarify migration routes and growth rates. Scale and otolith specimens from sampled salmon will permit interpretations of individual histories (Friedland and Haas 1996). Information from such specimens, taken in the course of the marine phase, will also help refine interpretations made from scales and otoliths collected from adults returning to rivers (Friedland et al. 1998). Sampling from gannets is likely to produce data on the biology of post-smolts at much lower cost than directed research cruises.

Studies in estuaries

Predation by birds and seals on outgoing smolts and by seals on returning adults has the potential to impact salmon populations. If predator harvest can be determined through diet studies and bioenergetic models (Cairns and Kerekes 2000, Hammill and Stenson 2000), and smolt output or adult returns can be measured through stock assessment programs, exploitation rate of local stocks can be calculated.

Double-crested cormorants breed colonially in coastal areas of southern Quebec, the Maritime Provinces, and New England. Several major salmon rivers, including the Saint John and the Restigouche, have large cormorant colonies near their mouths. Although cormorants commonly aggregate during runs of anadromous fish to feed, cormorant diet has not been recorded at or near large salmon rivers during the smolt run in eastern Canada. Cormorant diet can be determined from regurgitated boli (Johnstone et al. 1990) or, if necessary, from lethal stomach sampling. Bird numbers for use in bioenergetic models of total consumption can be derived from colony counts, or by estimating predator-days through air or vessel surveys, or counts from vantage points.

In Newfoundland, herring and great-blacked backed gulls suffered a loss of food supply following the decrease of offal availability due to the cod moratorium. Subsequently, anecdotal reports suggested that gulls increased their visitation of river mouths in spring, presumably to prey on runs of anadromous fishes (W.A. Montevecchi, pers. comm.). Diet of breeding gulls can be determined from regurgitations and from prey items dropped at colonies. Total food consumption can be determined as for cormorants above. Potential study sites include Rocky River and Exploits River, Newfoundland. Smolt runs of both of these rivers are assessed annually, and both are near gull colonies.

Seals frequent estuaries of rivers throughout northeastern North America, so there are numerous locations where exploitation rate of seals on salmon could potentially be calculated. Seal diet can be determined by analysis of scats collected from haul-out areas (da Silva and Neilson 1985), or from lethal sampling. Numbers of animals for input into bioenergetics models can be obtained from surveys of predator-days, although such data are likely to be less reliable than those for cormorants and gulls because seals are more difficult to count than birds.

Locating a predation study in the estuary of a salmon river does not guarantee that salmon contribution to predator diet can be readily and reliably determined. In the Miramichi estuary, returning adult salmon represent about 1% of total biomass of anadromous spawners (Chaput 1995). In general, biomass of salmon smolts and returning adults is probably a small fraction of total anadromous biomass in rivers with major smelt and gaspereau runs. This means that, if predators eat fish in proportion to their abundance, very large sample sizes would be required to accurately characterise the proportion of predator diet that is salmon. An additional problem with seal diet sampling by means of stomach or scat analysis is that seals do not necessarily consume the heads of large fish (Cairns and Reddin 2000), which means that methods based on detection of otoliths will underestimate salmon contribution to diet.

Attempts to reliably estimate exploitation rates of salmon in estuaries are most likely to be successful when there is a large run of smolts or adult salmon which occurs when abundance of other fishes is relatively low, and when predators are regularly present in substantial numbers. Exploitation rates estimated in such circumstances may be useful for understanding trophic ecology of salmon in the local river, but these rates should not be extrapolated to

broader geographic scales because the circumstances that make exploitation rate measurable probably also increase it above the level of "average" rivers.

Bigg et al. (1990) estimated consumption of returning adult salmon by pinnipeds by direct visual observation of predation events from boats and vantage points. This method avoids many of the uncertainties arising from diet analyses and bioenergetic modelling. However, it will work only if the geographic layout of the site, the clarity of the water, and the behaviour of the animals are suited to such observations. These conditions are probably not met in most estuaries in northeastern North America. The method also has its drawbacks. It may underestimate salmon predation if some attacks occur at depth or at night where they cannot be seen. Results of studies in which this method is applied may not be representative of estuaries in general, because the method is most likely to be successful when predation is relatively frequent.

Food-web analysis

The relation between predators and prey gives rise to the following questions, among others:

1) Is predator-induced mortality additive or compensatory?

2) Does predation by the predator depress populations by the amount removed, or is this consequence altered by such trophic mechanisms as suppression of competitors or removal of other predators?

3) Is predation a cause of population decrease?

4) Will predation prevent population recovery?

In freshwater, predation on juvenile salmonids may be compensatory rather than additive, because of self-thinning mechanisms that occur in populations with high initial densities (Grant 1993). It seems unlikely that self-thinning mechanisms operate in marine-phase salmon because salmon exist in such low numbers in the sea that changes in their populations are unlikely to affect resources available per fish (see Hansen 1993).

Beyond this, we can say little with certainty regarding cause-and-effect chains involving marine predation on salmon. In general, addition or removal of consumers does not cause linear, additive changes in food webs or prey mortality (Richardson and Threlkeld 1993). Predators rarely take only one prey species, and when their numbers are suppressed, predation may decrease on other species which are competitors or predators of the species of interest (Gulland 1987, Butterworth 1992, Lavigne 1996). This may in turn lead to lower populations of the species of interest, rather than the higher ones that are desired.

It is theoretically possible to determine cause-and-effect chains of marine predation by ecosystem experiments. However, Butterworth et al. (1998) calculated that to determine effects of a reduction in seal numbers on South African squid and anchovy stocks with a confidence level of 0.05, experiments would have to continue for 650 years. The experimental approach would seem to have little application to salmon on a northwest Atlantic scale. However, it is conceivable that an experiment in predator control could be designed in which predation on smolts or returning adults in estuaries is suppressed. Replicating the design across several estuaries would reduce the number of years to obtain statistically valid results. Such a program would not necessarily require lethal removals, if predation could be suppressed by scaring or other measures.

Mass-balance models of trophic interactions in the Northwest Atlantic are currently under development (Bundy et al. 2000). Such models begin with an initial statement of predator-prey interactions in an ecosystem; original input values are then adjusted until inputs and outputs are in balance. Yodzis (1998) has devised a method to predict ecosystem effects of perturbations in complex trophic webs from relatively simple data sets. Together, these approaches could potentially offer insights into the nature of relations between salmon and their marine predators. However, the utility of this method may be constrained by the difficulty (or impossibility) of obtaining accurate data on the contribution of salmon to the diets of most of its marine predators.

Recent theoretical literature (as cited above) has emphasized the possibility that reducing predator numbers may not lead to increases in the prey population. However, when a commercially fished species is in trouble, it is universally accepted that fisheries exploitation should decrease. Such a conclusion is drawn without consideration of whether the secondary effects of such action, such as reduction in bycatch removals of a competitor or a predator, might indirectly lead to increased mortality of the species of interest.

Given the complexity of marine food webs, cause-and-effect chains can be postulated that will support any given point of view. It is therefore particularly important that any use of food-web analysis to investigate the relations between salmon and their prey should begin with a neutrally objective approach, and avoid pre-conceived notions about whether predation does or does not negatively affect the prey population.

Discussion

This paper was written because managers and anglers have asked whether marine predators are causing the decline of Atlantic salmon returns, and if they are, what (if anything) could or should be done about it. This paper proposes several approaches to clarifying the complex relations between salmon and

their marine prey. None of these approaches will alone answer the pressing questions noted above. Instead, insights are most likely if a multi-pronged approach is taken. We need a fundamental understanding of the life history strategy of Atlantic salmon, and how salmon balance growth objectives and predator avoidance while at sea. We need to know more about the behaviour of salmon-predator interactions in the context of temperature, school formation, and the relative predation power of ectothermic and endothermic predators vs. ectothermic prey. We need to calculate exploitation rates where it is feasible to do so, and we need to fit available data into food-web models. This road may or may not lead to firm answers to the questions posed above, but if we do not take it, it is likely that the questions, and our ignorance, will persist.

Literature cited

Abrahams, M.V., and A. Sutterlin. 1999. The foraging and anti-predator behaviour of growth-enhanced transgenic Atlantic salmon. Anim. Behav. 58:933-942.

Amiro, P.G. 1998. The abundance of harp seals in the North Atlantic and recruitment of the North Atlantic stock of Atlantic salmon (*Salmo salar*). Can. Stock Assessment Secretariat Res. Doc. 98/84.

Anon. 1997. Impacts of California sea lions and Pacific harbor seals on salmonids and on the coastal ecosystems of Washington, Oregon, and California. NOAA Tech. Memorandum NMFS-NWFSC-28.

Anon. 1998. Report of the study group on ocean salmon tagging experiments with data logging tags. ICES CM 1998/G:17.

Anon. 1999a. Report of the working group on North Atlantic salmon. ICES CM 1999/ACFM:14.

Anon. 1999b. Report of the working group on marine mammal population dynamics and trophic interactions. ICES CM 1999/G:3. Ref. ACFM, ACME E.

Anon. 1999c. Report of the workshop on the usefullness of scale growth analyses and other measurements of condition in salmon. ICES CM 1999/G:15.

Anthony, V.C. 1994. The significance of predation on Atlantic salmon. Pp. 240-284 in S. Calabi and A. Stout (eds). A hard look at some tough issues. New England Salmon Management Conference, Danvers MA. Silver Quill Books, Camden, Maine.

Baum, Ed. 1997. Maine Atlantic salmon: a national treasure. Atlantic Salmon Unlimited, Hermon, Maine.

Bigg, M.A., G.M. Ellis, P. Cottrell, and L. Milette. 1990. Predation by harbour seals and sea lions on adult salmon in Comox Harbour and Cowichan Bay, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. No. 1769.

Blair, A.A. 1956. Atlantic salmon tagged in east coast Newfoundland waters at Bonavista. J. Fish. Res. Bd. Canada 13:219-232.

Boehlert, G.W. 1997. Application of acoustic and archival tags to assess estuarine, nearshore, and offshore habitat utilization and movement by salmonids. NOAA Tech. Memorandum NMFS-SWFSC-236.

Booth, R.K., R.S. Mckinley, F. Okland, and M.M. Sisak. 1997. In situ measurement of swimming performance of wild Atlantic salmon (*Salmo salar*) using radio transmitted electromyogram signals. Aquat. Living Res. 10:213-219.

Bundy, A., G.R. Lilly, and P.A. Shelton. 2000. A mass balance model of the Newfoundland-Labrador Shelf. Can. Tech. Rep. Fish. Aquat Sci. 2310.

Butterworth, D.S. 1992. Will more seals result in reduced fishing quotas? S. Afr. J. Fish. Sci. 88:414-416.

Butterworth, D.S., D.C. Duffy, P.B. Best, and M.O. Bergh. 1998. On the scientific basis for reducing the South African seal population. S. Afr. J. Sci. 84:179-188.

Cairns, D.K. 1998. Diet of cormorants, mergansers, and kingfishers in eastern North America. Can. Tech. Rep. Fish. Aquat. Sci. No. 2225.

Cairns, D.K., and J.J. Kerekes. 2000. Fish harvest by common loons and common mergansers in Kejimkujik National Park, Nova Scotia, Canada, as estimated by bioenergetic modeling. Pp. 125-135 in F.A. Comin, J.A. Herrera and J. Ramirez (eds.). Limnology and aquatic birds: monitoring, modelling, and management. Universidad Autonoma de Yucatan, Mérida (Mexico).

Cairns, D.K., and D.G. Reddin. 2000. The potential impact of seal and seabird predation on North American Atlantic salmon. Can. Stock Assess. Secretariat Res. Doc. 2000/12.

Chaput, G.J. 1995. Temporal distribution, spatial distribution, and abundance of diadromous fish in the Miramichi River watershed. Can. Spec. Publ. Fish. Aquat. Sci. 123:121-139.

Chaput, G., D. Moore, J. Hayward, J. Shaesgreen, and B. Dube. 1999. Stock status of Atlantic salmon (*Salmo salar*) in the Miramichi River, 1999. Can. Stock Assess. Secretariat Res. Doc. 99/93.

Colbourne E. 1999. Oceanographic conditions in NAFO Divisions 2J 3KLMNO during 1998 with comparisons to the long-term (1961-1990) average. DFO Canadian Stock Assessment Secretariat Research Document 99/48, 46 p.

da Silva, J. and J.D. Neilson. 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Can. J. Fish. Aquat. Sci. 42:1439-1442.

Dempson, J.B., and D.G. Reddin. 2000. Newfoundland and Labrador Atlantic salmon (*Salmo salar*) stock status summary for 1999, and methods to addess possible causes for continuing low abundance and survival. Can. Stock Assess. Secretariat Res. Doc. 2000/112.

Diamond, A.W., A.J. Gaston and R.G.B. Brown, R.G.B. 1993. Studies of high-latitude seabirds. 3. A model of the energy demands of the seabirds of eastern and Arctic Canada. Can. Wildl. Serv. Occ. Paper no. 77. 39 pp.

Duffy, D.C., Schneider, D.C. 1994. Seabird-fishery interactions: a manager's guide. In D.N. Nettleship, J. Burger and M. Gochfeld (eds.). Seabirds on islands: threats, case studies, and action plans. BirdLife Conservation Series No. 1:26-38.

Dutil, J.D. and J.M. Coutu. 1988. Early marine life of Atlantic salmon, *Salmo salar*, postsmolts in the northern Gulf of St. Lawrence. Fish. Bull. 86:197-212.

Evans, D.O. 1990. Metabolic thermal compensation by rainbow trout: effects on standard metabolic rate and potential usable power. Trans. Am. Fish. Soc. 119:585-600.

Fiscus, C.H. 1980. Marine mammal-salmonid interactions: a review. Pp. 121-132 in W.J. McNeil and D.C. Himsworth (eds.). Salmonid ecosystems of the North Pacific. Oregon State Univ., Corvallis.

Fleming, I.A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Can. J. Fish. Aquat. Sci 55(Suppl. 1):59-76.

Fontaine, P.-M., M.O. Hammill, C. Barrette, and M.C. Kingsley. 1994. Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the Northern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 51:172-178.

Fraser, N.H.C., J. Heggenes, N.B. Metcalfe, and J.E. Thorpe. 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. Can. J. Zool. 73:446-451 1995.

Frederick, P.C., and W.F. Loftus. 1993. Responses of marsh fishes and breeding wading birds to low temperatures: A possible behavioral link between predator and prey. Estuaries 16:216-222.

Friedland, K.D., J.-D. Dutil, and T. Sadusky. 1998. Growth patterns in postsmolts and the nature of the marine juvenile nursery for Atlantic salmon, *Salmo salar*. Fish. Bull. 97:472-481.

Friedland, K.D., and R.E. Haas. 1996. Marine post-smolt growth and age at maturity of Atlantic salmon. J. Fish Biol. 48:1-15.

Fryer, J.K. 1998. Frequency of pinniped-caused scars and wounds on adult spring-summer chinook and sockeye salmon returning to the Columbia River. N. Am. J. Fish. Manage. 18:46-51.

Gotceitas, V., and J.-G. J. Godin. 1993. Effects of aerial and in-stream threat of predation on foraging by juvenile Atlantic salmon (*Salmo salar*). Pp. 35-41 in R.J. Gibson and R.E. Cutting (eds.). Production of juvenile Atlantic salmon, *Salmo salar*. Can. Spec. Publ. Fish. Aquat. Sci. 118.

Grant, J.W.A. 1993. Self-thinning in stream-dwelling salmonids. Can. Spec. Publ. Fish. Aquat. Sci. 118:99-102.

Greenwood, M.F.D., and N.B. Metcalfe. 1998. Minnows become nocturnal at low temperatures. J. Fish Biol. 53:25-32.]

Gulland, J.A. 1987. Seals and fisheries: a case for predator control? Trends Ecol. Evol. 2:102-104.

Hammill, M.O., and G.B. Stenson. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. J. Northw Atl. Fish. Sci. 26:1-23.

Hansen, L.P. 1993. Movement and migration of salmon at sea. Pp. 26-39 in D. Mills, Salmon in the sea and new enhancement strategies. Fishing News Books, Oxford Press.

Harmon, J.R., K.L. Thomas, K.W. McIntyre, and N.N. Paasch. 1994. Prevalence of marine-mammal tooth and claw abrasions on adult anadromous salmonids returning to the Snake River. N. Am. J. Fish. Manage. 14:661-663.

Harwood, J. 1984. Seals and fisheries. Mar. Pollut. Bull. 15:426-429.

Harwood, J., and J.J.D. Greenwood. 1985. Competition between British grey seals and fisheries. Pp. 153-169 in J.E. Boddingtons, R.J.H. Beverton, and D.M. Lavigne (eds.). Marine mammals and fisheries. George Allen and Unwin, London.

Holm, M., E. Ona, I. Huse, O.T. Skilbrei, and K.E. Joerstad. 1992. Migratory behaviour of individuals and schools of Atlantic salmon postsmolts observed by hydroacoustic methods. Nord. J. Freshwat. Res. 69:98.

Holst, J.C., R. Shelton, M. Holm, and L.P. Hansen. 2000. Distribution and possible migration routes of post-smolt Atlantic salmon in the north-east Atlantic. Pp. 65-74 in Mills, D. (ed.). The ocean life of Atlantic salmon: environmental and biological factors influencing survival. Fishing News Books, Oxford.

Hutchings, J.A., and M.E.B. Jones. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 55(Suppl. 1):22-47.

IPCC 1995. The science of climate change. Contribution of Working Group I to the Second Assessment Report of the Intergovenmental Panel on Climate Change. Cambridge University Press.

Joerstad, K.E., O.T. Skilbrei, M. Holm, O Skaala, and E. Farestveit. 1994. Video-documentation of salmon smolt behavior comparison between releases from a river and from a small coastal bay. Nord. J. Freshwat. Res. 69:102.

Johnston, I.A., T.P. Johnston, and J.C. Battram. 1991. Low temperature limits burst swimming performance in Antarctic fish. Pp. 179-190 in B. di Presco, B. Maresca, and B. Tota (eds.). The biology of Antarctic fish. Springer-Verlag, Berlin.

Johnstone, I.G., M.P. Harris, S. Wanless, and J.A. Graves. 1990. The usefulness of pellets for assessing the diet of adult shags Phalacrocorax aristotelis. Bird Study 37:5-11.

Juell, J.-E. 1995. The behaviour of Atlantic salmon in relation to efficient cage-rearing. Rev. Fish Biol. Fish. 5:320-335.

Kennedy, G.J.A., and J.E. Greer. 1988. Predation by cormorants, Phalacrocorax carbo (L.), on the salmonid population of an Irish river. Aquaculture Fish. Manage. 19:159-170.

Kenney, R.D., G.P. Scott, T.J. Thomson, and H.E. Winn. 1997. Estimates of prey consumption and trophic impacts of cetaceans in the USA northeast continental shelf ecosystem. J. Northw. Atl. Fish. Sci. 22:155-171.

Krause, J., G.D. Ruxton, and D. Rubenstein. 1998. Is there always an influence of shoal size on predator hunting success? J. Fish Biol. 52:494-501.

Lavigne, D.M. 1996. Ecological interactions between marine mammals, commercial fisheries, and their prey: unravelling the tangled web. Canadian Wildlife Service Occ. Paper 91:59-71.

Lorenzen, K. 1996. The relation between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J. Fish. Biol. 49:627-647.

Montevecchi, W.A., D.K. Cairns, and V.L. Birt. 1988. Migration of post-smolt Atlantic salmon, *Salmo salar*, off northeastern Newfoundland, as inferred by tag recoveries in a seabird colony. Can. J. Fish. Aquat. Sci. 45:568-571.

Montevecchi, W.A., D.K. Cairns, and R.A. Myers. Predation on Atlantic salmon by northern gannets in the northwest Atlantic. Submitted to Can. J. Fish. Aquat. Sci.

Nash, C.E., R.N. Iwamoto, and C.V.W. Mahnken. 2000. Aquaculture risk management and marine mammal interactions in the Pacific Northwest. Aquaculture 183:307-323.

O'Neill, S., J. Ritter, and K. Robichaud-Leblanc. 2000. Proceedings of a workshop on research strategies into the causes of declining salmon returns to North American rivers. Can. Stock Assessment Secretariat Proceedings Ser. 2000/18.

Parkinson, E.A. 1991. Impaired school formation at low density: A mechanism for depensatory mortality in sockeye salmon. Fish. Manage. Rep. (Province of British Columbia). No. 99.

Peuhkuri, N. 1997. Size-assortative shoaling in fish: the effect of oddity on foraging behaviour. Anim. Behav. 54:271-278.

Pierce, G.J., J.S.W. Diack, and P.R. Boyle. 1990. Application of serological methods to identification of fish prey in diets of seals and dolphins. J. Exp. Mar. Biol. Ecol. 137:123-140.

Pierce, G.J., J.R.G. Hislop, and T.J. Carter. 1997. Interactions between seals and salmon in northeast Scotland. Salmon Net 28:49-55.

Pierce, G.J., P.M. Thompson, A. Miller, J.S.W. Diack, D. Miller, and P.R. Boyle. 1991. Seasonal variation in the diet of common seals (*Phoca vitulina*) in the Moray Firth area of Scotland. J. Zool. (Lond.). 223:641-652.

Rae, B.B. 1973. Further observations on the food of seals. J. Zool. (Lond.). 169:287-297.

Rae, B.B., and W.M. Shearer. 1965. Seal damage to salmon fisheries. Mar. Res. 2:1-39.

Reddin, D.G., J.B. Dempson, P. Downton, C.C. Mullins, and K.D. Friedland. 1999. Migration of Atlantic salmon kelts (*Salmo salar* L.) in relation to sea water temperature in Newfoundland, 1998. Can. Stock Assess. Secretariat Res. Doc. 99/85.

Reitan, O., N.A. Hvidsten, and L.P. Hansen. 1987. Bird predation on hatchery reared Atlantic salmon smolts, *Salmo salar* L., released in the River Eira, Norway. Fauna norv. Ser. A 8:35-38.

Richardson, W.B., and S.T Threlkeld. 1993. Complex interactions of multiple aquatic consumers: an experimental mesocosm manipulation. Can. J. Fish. Aquat. Sci. 50:29-42.

Roby, D. 1997. Salmon restoration and fish-eating birds in the Columbia Basin: on a collision course? Oregon State University Fisheries and Wildlife Dept. News and Views, Winter 1997. Pp. 6-7.

Scott, W., and M. Scott. 1988. Atlantic fishes of Canada. University of Toronto Press.

Sigurjonsson, J., and G.A. Vikingsson. 1998. Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. J. Northw. Atl. Fish. Sci. 22:271-287.

Sogard, S.M., and B.L. Olla. 1997. The influence of hunger and predation risk on group cohesion in a pelagic fish, walleye pollack *Theragra chalcogramma*. Environ. Biol. Fish. 50:405-413.

Sturlaugsson, J. 1995. Migration study on homing of Atlantic salmon (*Salmo salar* L.) in coastal waters W-Iceland. ICES CM 1995/M:17.

Thompson, P.M , and F. MacKay. 1999. Pattern and prevalence of predator damage on adult Atlantic salmon, *Salmo salar* L., returning to a river system in north-east Scotland. Fish. Manage. Ecol. 6:335-343.

Tomilin, A.G. 1957. Mammals of the U.S.S.R. and adjacent countries. Israel Program for Scientific Translations, Washington.

Valdimarsson, S.K, and N.B. Metcalfe. 1997. Shelter selection in juvenile Atlantic salmon, or why do salmon seek shelter in winter? J. Fish. Biol. 52:42-49.

Valle, E. 1985. Predation of birds on salmon and sea trout smolts and post-smolts. ICES CM 1985/M:22.

Wanless, S. 1984. The growth and food of young gannets *Sula bassana* on Ailsa Craig. Seabird 7:62-70.

Wardle, C.S. 1980. Effects of temperature on the maximum swimming speed of fishes. Pp. 519-531 IN M.A. Ali (ed.). Environmental physiology of fishes. Plenum, N.Y.

Welch, D.W., L. Margolis, M.A. Henderson, and S. McKinnell. 1991. Evidence for attacks by the bathypelagic fish *Anotopterus pharao* (Myctophiformes) on Pacific salmon (*Oncorhynchus* spp.). Can. J. Fish. Aquat. Sci. 48:2403-2407.

Yodzis, P. 1998. Local trophodynamics and the interactions of marine mammals and fisheries in the Benguela system. J. Anim. Ecol. 67:635-658.